The diet of pine martens (*Martes martes*) with reference to squirrel predation in Loch lomond and The Trossachs National Park, Scotland

William D. Paterson¹ and Gavin Skipper²

¹Division of Environmental and Evolutionary Biology, Institute of Biomedical & Life Sciences, University of Glasgow, Glasgow G12 8QQ E-mail: 0211087p@student.gla.ac.uk

²Loch Lomond & The Trossachs National Park Authority, National Park Headquarters, Balloch Road, Balloch, Alexandria G83 8BF E-mail: gavin.skipper@lochlomond-trossachs.org

ABSTRACT

In this study into the diet of pine martens, scats were collected from four sites in the Loch Lomond and The Trossachs National Park, Scotland. Analysis of prey remains in scat samples showed that there was no evidence of squirrel predation at any of the chosen study sites. This was despite population estimates using cone feeding transects indicating that squirrels were present within pine marten ranges in at least two different sites. Hair tube surveys were also carried out which confirmed the presence of red squirrels in Glenbranter. Field voles were found in a higher proportion of scats in Glenbranter and Auchineden than at Sallochy and Duke's Pass which may be explained by seasonal variation in numbers. Field voles were the most frequent prey identified while plant material that included seasonally abundant rowan berries was found in a higher proportion of scats at two sites. These findings are in line with other studies of pine marten diet in Scotland that show the field vole to be the preferred prey species of pine martens occurring in a higher proportion of scats from the winter onwards and that fruits and berries occur in a higher proportion of scats in summer and autumn. This study suggests that pine martens are not preying upon squirrels in the National Park, possibly because squirrels were found to be absent or occurred at very low densities in the chosen study sites.

INTRODUCTION

Pine martens (*Martes martes*) are distributed throughout central and northern Europe as well as in Britain (MacDonald, 2001). However, pine martens live at low densities making them intrinsically vulnerable to disturbances such as habitat destruction and hunting pressure (Morris, 1993). Unfortunately, they have endured both of these factors which almost led to the extinction of pine martens in the UK (Bright, 2000; Webster, 2001). Pine martens have been increasing in number from around 1926 onwards (Lockie, 1964). Increased public awareness and reafforestation has led to their recovery in Scotland, with an estimated population of 3500 (Battersby, 2005).

Native red squirrel (*Sciurus vulgaris*) populations have been in decline in Britain, particularly in the last 50 years (Pepper & Patterson, 1998) so that they are now only considered common on a local scale in parts of Scotland (Arnold, 1993). Introduced North American grey squirrels (*Sciurus carolinensis*) have displaced red squirrels where the two have met as they appear to compete for food (Pepper & Patterson, 1998). However, red squirrels can outcompete grey squirrels in the right conditions such as in pure coniferous forest where the dietary requirements of grey squirrels are less readily met (Gurnell *et al*, 2001; Morris, 1993). Scotland provides large areas of conifer plantations into which red squirrel populations have contracted (Holm, 1987).

There is anecdotal evidence that pine martens preferentially take grey squirrels over red squirrels. This may be attributable to better predator avoidance by red squirrels that are able to reach finer branches (Kenward et al, 1998). Conservation measures that benefited pine martens could therefore indirectly benefit the red squirrel by limiting the spread of grey squirrels in Scotland. There have been studies in Finland (Nyholm, 1970), Sweden (de Jounge, 1981) and Germany (Russell & Storch, 2004) that have demonstrated that squirrels can make up a large proportion of the total diet of pine martens. The National Park represents the first place in Britain where the recovering pine marten population has come into contact with an established population of the alien grey squirrel (Mitchell, 2005). The possibility that the pine marten could prove to be an effective check on grey squirrel abundance is thus worthy of detailed examination.

The principal aim of this study was to investigate the occurrence of red and grey squirrels in the diet of pine martens. This study also aimed to determine whether or not there was a relationship between squirrel abundance and the occurrence of squirrels in the pine marten diet. This study was carried out within Loch Lomond and The Trossachs National Park in Scotland where red squirrels are of particular conservation concern as they are considered an iconic species important for attracting visitors. The pine marten is not

considered a priority species for conservation but is an important component of the National Park's biodiversity.

METHODS

From previous local knowledge scats were collected from four sites: Auchineden (NS 508804), Sallochy (NS 389951), Duke's Pass (NN 515031) and

Glenbranter (NS 113987) (Figure 1). Auchineden and Sallochy were considered to be grey squirrel sites and Duke's Pass and Glenbranter were red squirrel sites. Scats from Auchineden were collected in May 2005. Scats from Sallochy, Duke's Pass and Glenbranter were collected between 24 - 29 Oct. 2006, 5 - 12 Nov. 2006 and 14 Nov. 2006 - 7 Jan. 2007, respectively.

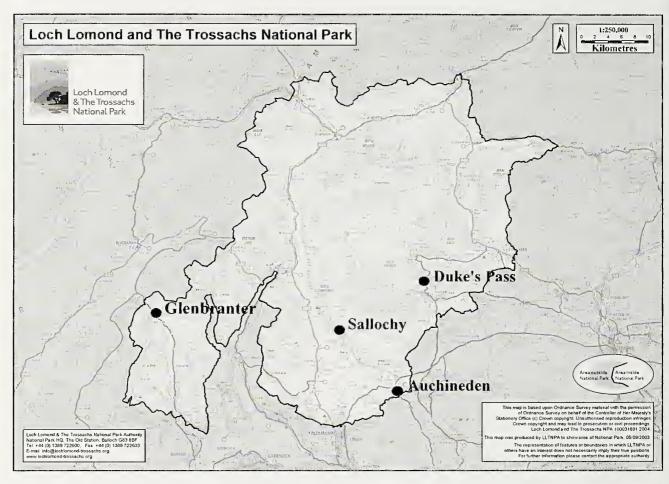


Fig. 1. This map shows the boundary of Loch Lomond and The Trossachs National Park. Also shown are the locations of the four study sites Auchineden, Duke's Pass, Glenbranter and Sallochy

Cone feeding transects were carried out in order to estimate the density of squirrels at each site. This was done at Sallochy, Duke's Pass and Glenbranter but was not undertaken at the Auchineden site due to time constraints. Fourteen transects at each of the three sampling sites (Sallochy, Duke's Pass and Glenbranter) gave a total of 42 transects overall. Transects were completed according to Gurnell *et al* (2001) and calculations of squirrel densities were based on derived energy values of the cones of particular tree species. Trees and their cones were identified using an appropriate key (Harris and Harris, 2002).

Hair tube surveys were carried out at Sallochy, Duke's Pass and Glenbranter according to Gurnell *et al* (2001) in order to determine which species of squirrel was present at each site. Ten hair tubes were set out at each site. Due to time constraints no hair tube survey was done at Auchineden. Hair tubes were collected after 2 weeks. Hairs were identified as far as possible using appropriate keys (Day, 1966; Teerink, 2003).

Scats were collected from forestry roads and paths and identified using a guide to mammal tracks and signs (Bang and Dahlstrøm, 2001). The location of scats was recorded using a handheld GPS (eTrex®, Taipei, Taiwan). Scats were then taken back to the lab and frozen at -20°C for later examination. A total of 30 scats were collected at each study site.

Scats were defrosted and examined using a dissecting microscope (Olympus SD30, Nagano, Japan). Any identifiable remains were picked out and washed in a solution of biological detergent (Biotex®, Blumøller Ltd., Denmark). Seeds, nuts and berries were identified as far as possible using Ross-Craig (1956) and invertebrate remains were identified as far as possible using Chinery (1993). Scats with hairs in them were left overnight in a solution of biological detergent in order to avoid damaging hairs.

Hair identification

A 15% gelatine stock solution was made using gelatine powder (BDH Chemicals Ltd, Dorset, England) and distilled water, with a few crystals of thymol as a preservative. The solution was then poured over a cover glass and left to dry. Clean, dry hairs were prepared for making impressions by placing them in a plastic hand sieve and soaking them in a bath of Histo-Clear® (National Diagnostics, Atlanta, USA) for at least 5 minutes to remove the fatty, waxy layer that surrounds hairs, allowing for a better impression of the cuticular scale to be made. Hairs were then left to dry overnight. Previously prepared cover slides could then be made ready simply by brushing tepid water over the gelatine layer using an artist's paintbrush. The prepared hairs were laid on the cover slide while applying a small amount of pressure to embed the hair in the gelatine. Cover slides with cuticular impressions on them were then turned over and placed on an excavated glass block. This allowed for the negative of the impression to be viewed at 400x magnification using a binocular microscope (Leitz®, S-M-Lux Brightfield, Wetzlar, Germany). Cuticular impressions were identified as far as possible using appropriate keys (Day, 1966; Teerink, 2003).

Individual guard hairs or groups of guard hairs were placed on a strip of balsa wood. A cyanoacrylate gel adhesive (Rite-Lok®, Georgia, USA) was then laid over the top, embedding the hair(s) in the adhesive. When the balsa wood preparations were completely dry and hardened, thin cross-sections were made with a razor blade. Cross-sections were then mounted dry on a glass slide with a cover slide laid on top. This allowed for each cross-section to be examined at 400x magnification. Cross-sections were identified as far as possible using appropriate keys (Day, 1966; Teerink, 2003).

A reference collection of hairs was used to check hair identification methods. Reference hairs were from museum specimens. These included hairs from the field vole (*Microtus agrestis*), the European rabbit (*Oryctolagus cuniculus*), pine marten, brown hare (*Lepus europaeus*), common mole (*Talpa europea*), common shrew (*Sorex araneus*) and grey squirrel. Hairs were also provided from trapped specimens of the bank vole (*Clethrionomys glareolus*) and the wood mouse (*Apodemus sylvaticus*). Hairs of the red squirrel were taken from a road kill. Cuticular impressions, medullar impressions and cross-sections were made of the hairs of all these species.

STATISTICAL ANALYSIS

Chi-square tests were used to compare the differences between sites in terms of scat composition as the data collected were in the form of counts of categories. Berries, nuts and vegetation were grouped together as 'Plant material'. Birds, mammals and beetles were grouped together in order to compare between sites the number of scats that contained animals. The number of scats containing only mammals was then compared between sites. It was not possible to determine whether

or not the field vole was preferred over the bank vole at any of the sites studied as more than 20% of the expected values were less than five.

The median number of squirreled cones was compared between Sallochy, Duke's Pass and Glenbranter using a Kruskall-Wallis test. A non-parametric test was chosen because the variances between sites showed large differences for ANOVA.

The median altitude of scats collected was compared between Sallochy, Duke's Pass and Glenbranter using a Kruskall-Wallis test. A non-parametric test was chosen because the variances between sites showed large differences for ANOVA. The proportion of scats containing mammals was also compared between height categories (< 60m, 60-120m, 120-180m, 180-240m and 240-300m). A Chi-squared test was carried out on the pooled data from Sallochy, Duke's Pass and Glenbranter as individually the data were too small to carry out tests for differences between each site.

Sample sizes from hair tubes were too small for statistical tests.

RESULTS

Diet

Vegetation was found in many of the scats in this study but only rowan berries (*Sorbus aucuparia*) were positively identified to species level. Seeds and nuts were also found in several scats. The only type of invertebrates found were beetles from the family Geotrupidae (dor beetles). Bird feathers were found in a number of scats but were not identified to species level due to uncertainty about making positive determinations. Mammal remains consisted of bones, teeth and hair. Mammals identified in the scats in this study included the field vole, the bank vole and the wood mouse.

There was a highly significant difference between the four sites in the proportion of scats that contained plant material (χ^2 d.f. = 3, P < 0.01). Duke's Pass and Sallochy both had plant material in 100% of scats collected while scats collected in Glenbranter and Auchineden had plant material in 17% and 73% of scats respectively (Figure 2). It was found that there was no significant difference between sites in the proportion of scats that contained birds, mammals or beetles (χ^2 d.f. = 3, P > 0.05). Birds, mammals or beetles were found in 83% of scats at Glenbranter and 77% of scats at Auchineden. Birds, mammals or beetles were found in 47% of scats at both Sallochy and Duke's Pass (Figure 2). There was a highly significant difference in the proportion of scats containing mammals between sites (χ^2 d.f. = 3, P < 0.01). Glenbranter and Auchineden had high proportions of mammals in scats collected with 83% and 70% respectively. Sallochy and Duke's Pass both had lower proportions of mammals in scats collected, with mammals occuring in 27% and 23% of scats respectively (Fig. 2).

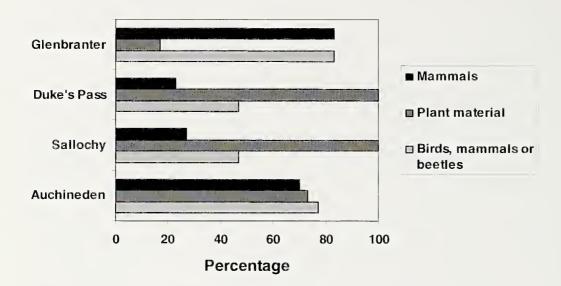


Fig. 2. This figure shows the differences between sites in terms of the percentage of scats that contained mammals, plant material and birds, mammals or beetles.

No squirrel remains were found in any of the scats at any of the sites in this study. It was found that there was a highly significant difference between sites in the proportion of scats containing the field vole (χ^2 d.f. = 3, P < 0.01). The field vole was found in 47% of scats in Auchineden and 37% of scats in Glenbranter. Proportions of scats containing the field vole were much lower in Sallochy and Duke's Pass being found in 10% and 7% of scats respectively (Figure 3). There was no significant difference between sites in the proportion of scats containing the bank vole (γ^2 d.f. = 3, P > 0.05). The highest proportion of the bank vole was in Glenbranter being found in 43% of scats. Proportions of scats containing the bank vole were lower in Auchineden, Sallochy and Duke's Pass at 17%, 20% and 17% respectively (Figure 3). The wood mouse was found in 10% of scats both at Auchineden and Glenbranter but was not present in any of the scats collected from Sallochy or Duke's Pass. The data for the wood mouse were too small to analyse statistically (Figure 3).

Squirreled cones

There was a highly significant difference in the median number of squirreled cones, i.e. cones eaten by squirrels, between Sallochy, Duke's Pass and Glenbranter (H = 27.43, d.f. = 2, p < 0.01). Duke's Pass had the highest squirreled cone count, Glenbranter the second highest while no squirreled cones were found in any of the 14 transects done at Sallochy. Using this data it was calculated from the number of squirreled cones in each transect that the area studied in Sallochy supported no squirrels, that the area studied in Duke's Pass supported 19 squirrels and that the area studied in Glenbranter supported 3 squirrels. This

equates to 0, 0.08 and 0.02 squirrels ha⁻¹ in Sallochy, Duke's Pass and Glenbranter respectively.

Scat locations

There was a highly significant difference in the median altitude at which scats were collected at Duke's Pass, Sallochy and Glenbranter (H = 57.57, d.f. = 2, p < 0.01). Median altitude of scat locations was greatest in Duke's Pass at 268m compared to Sallochy and Glenbranter at 135m and 119m respectively.

The proportions of scats containing small mammals were compared for the different height categories. It was found that when scats containing small mammal species were pooled for Sallochy, Duke's Pass and Glenbranter there was a highly significant difference between height categories (χ^2 d.f. = 4, P < 0.01). More scats containing small mammals were found at elevations of between 60-180m than at lower or higher elevations (Figure 4). Comparisons could not be made between sites as the sample sizes were too small.

Hair tubes

Only the Glenbranter site provided hair samples from a single hair tube that were identified as being from a red squirrel. No grey squirrel hairs were found in any of the hair tubes at any of the study sites. Wood mouse hairs were found in a single hair tube in Glenbranter and pine marten hairs were found in a single hair tube in Duke's Pass. None of the hair tubes in Sallochy contained hair samples.

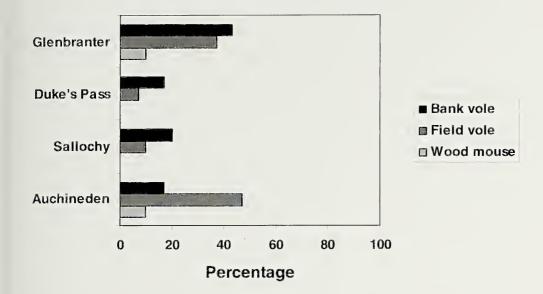


Fig. 3. This figure shows the differences between sites in terms of the percentage of scats that contained the bank vole, the field and the wood mouse.

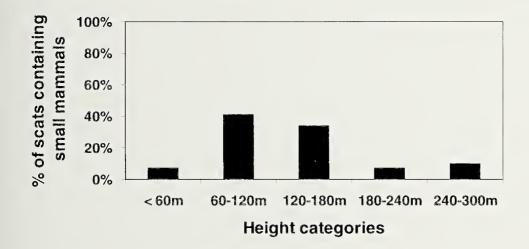


Fig. 4. This figure shows the altitude at which scats containing small mammals (n = 41) were found in this study. Small mammals include the field vole, the bank vole and the wood mouse.

DISCUSSION

Pine marten - squirrel interactions

The absence of squirrel predation by pine martens at all of the sites in this study was in line with findings of similar studies previously undertaken in Scotland (Gurnell *et al*, 1994; Lockie, 1964). The fact that no squirrels were found in the diet of pine martens in Sallochy is perhaps unsurprising as it would seem from the results of this study that there are few, if any, squirrels in the coniferous woods there. Pine martens have been impacting on the East Lomondside Fauna since at least 1989 (Trubridge, 1993) which may account for grey squirrels having been in decline in the area around Sallochy in the last 6 to 10 years (Hannan,

A., pers. comm., 2006). However, they are still present in very small numbers in adjacent areas as was verified by two confirmed sightings in 2005 (Skipper, G., pers. comm., 2006). The Rowardennan area contains prime habitat for grey squirrels consisting mostly of oak woodland. However, this study was done in the coniferous woodland nearby where conditions for grey squirrels would be less than optimal. The results of this study would suggest that any remaining grey squirrels may have retreated into surrounding areas where their optimal habitat, deciduous broadleaf woodland (Kenward et al, 1998, Pepper & Patterson, 1988), can be found. That there is no evidence of red squirrels at Sallochy may be due to greys having displaced them through competition for food in the past. It has also

been proposed that grey squirrels have since succumbed to a high predation pressure by pine martens in Sallochy (Anderson, D., pers. comm., 2006; Skipper, G., pers. comm., 2006). This could explain why no evidence of squirrel predation was found in the scat samples collected there.

Red squirrels are thought to be resident in the Glenbranter site in this study (McCahon, M., pers. comm., 2006), which was confirmed by the hair tube survey carried out there. However, the area studied was calculated to only support 0.02 squirrels ha⁻¹ according to cone feeding surveys. The density at which red squirrels were found at Glenbranter was particularly low, as elsewhere in Europe they can be found in densities of between 0.39-0.58 squirrels ha⁻¹ (Wauters et al, 2001). The apparent low density of red squirrels at Glenbranter may mean that encounters with pine martens would only happen occasionally. Red squirrel predation would thus be incidental and rare in occurrence meaning that on the scale of the present study it would be fortunate to discover red squirrel remains in scat samples. Duke's Pass had the highest squirrel density of 0.08 squirrels ha⁻¹ which again, was relatively low compared to the study by Wauters et al (2001). The Duke's Pass site was therefore the most likely candidate for pine marten predation on squirrels. However, this was not found to be the case and therefore the lack of evidence for squirrel predation at all sites may have been due to the low densities at which squirrels were found.

It appears there is an alternative food source that occurs in sufficient abundance at each of the four sites. This could be freeing pine martens from the necessity to switch to squirrel predation, which would be more costly in terms of energy invested in hunting them (Balharry, 1993). It has been well documented that the field vole is the preferred prey of pine martens in Scotland (Balharry, 1993; Halliwell, 1993; Lockie, 1964) and so if numbers of field voles were relatively abundant at the four sites they would certainly be preferred over squirrels. Field voles were found in a significantly higher proportion of scats in Glenbranter and Auchineden than at Salloehy and Duke's Pass suggesting they may be more abundant in these areas.

Other prey items

Pine martens rely on voles as an integral part of their diet at certain times of the year (Bierman *et al*, 2006; Gurnell *et al*, 1994; Helldin, 1999). In a study by Erlinge *et al* (1983) in Sweden, predation on voles had a strong seasonal fluctuation. The results of this study would agree with this as there was a significantly higher incidence of field voles in scats collected in Glenbranter in mid-November which was still evident in scats collected in Auchineden in May.

Pine martens were eating significantly more berries, nuts and/or seeds in Sallochy in October and Duke's Pass in early November. This could be a reflection of these types of food becoming super abundant at that time of year. The incidence of berries, nuts and/or

seeds was also quite high in Auchineden in May which may indicate that vole numbers were relatively low, causing pine martens to supplement their diet. The importance of eating rowan berries may be that they are a rich source of vitamin C (Harris & Harris, 2002) which pine martens could possibly lack if prey animals were lacking in their diet. What is notable about this point is that if field vole numbers were reduced at certain times of the year then it might be expected that pine martens would be more inclined to prey upon squirrels as an alternative food source which was found to be the case by Helldin (1999). However, this was not found to be evident in this study.

Conservation of pine martens and red squirrels

Any measures aimed at assisting in the recovery of pine martens in Scotland may be in conflict with the conservation of red squirrels (Balharry, 1993). Grey squirrel predation by pine martens would be beneficial to red squirrels as it would remove competition with grey squirrels and reduce the risk of contracting squirrel pox virus. However, it was found by Halliwell (1993) that in forests where pine martens had been present for more than ten years, red squirrel numbers were reduced and their recruitment rate was lower than in forests recently colonised by pine martens. Therefore, it is worth noting that while pine martens may have value as a biological control of grey squirrels, they may also be detrimental to the recovery of the National Park's red squirrel population.

Pine marten scats containing small mammals in this study were mostly deposited at altitudes of between 60-180m. It could be that pine martens are concentrating their activity at those altitudes because this is also where small mammals are abundant. Conservation measures aimed at maintaining small mammal populations could therefore discourage pine martens from switching to alternative food sources such as squirrels in other parts of the National Park. It is thought, for example, that the field vole is in decline in Britain due to its preferred habitat of rough grassland being reduced by modern agricultural practices (Battersby, 2005). It would be advisable then that rough grassland or more open areas of forest are incorporated into future land management plans in the National Park. This would increase prey abundance for pine martens and possibly reduce the risk of red squirrel predation.

Further research

The fact that this study found no squirrels in the diet of pine martens may simply be that the density of squirrels was not high enough at any of the sites. Similarly, the density of other prey species such as the field vole, bank vole and the wood mouse may fluctuate in numbers making population estimates of these species essential in determining what is available to pine martens relative to what is found in their diet. Future studies that analyse the dietary composition of pine martens should be carried out alongside population estimates of all prey species as pine martens will switch their diet in line with which prey species is

most abundant at the time. A study site where red and grey squirrels co-exist in the presence of pine martens could also help determine whether or not one species of squirrel was preferred.

CONCLUSIONS

The results of this study suggest that squirrel predation by pine martens is not occurring at any of the chosen study sites. It is apparent from local information however, that significant declines in the West of Scotland squirrel populations had occurred before the present study began. It may be then that evidence of squirrel predation was not found simply because squirrels are not found in sufficient numbers to be evident in the diet of pine martens. It is clear from reviewing the literature that estimating the population of all prey items that might occur in the diet of pine martens would be the best approach to any future studies. This would go some way towards explaining any seasonal differences in the relative abundance of certain prey items. This would also provide evidence to explain why squirrels may be absent in the diet of pine martens, as the tendency of pine martens to switch to alternative food sources as they become more abundant may negate any possibility of squirrel predation within the National Park. It is clear that while the conservation of both pine martens and red squirrels is in the best interest of maintaining the biodiversity of the National Park, there may be conflicting issues involved in areas where pine martens may prey upon red squirrels. Further research is needed to confirm anecdotal evidence that pine martens preferentially prey on grey squirrels over red squirrels.

ACKNOWLEDGEMENTS

This project was undertaken as a final year dissertation by WP for a BSc in Zoology at the University of Glasgow.

We would like to thank Dr. Dominic McCafferty for his support and advice throughout this project. We are grateful to Pat Mclaughlin, Irene Leighton and Graham Adam for their help in providing lab space and equipment. We are grateful to Prof. Graeme Ruxton for his advice on statistics and also Prof. David Houston and Maggie Reilly for providing reference hairs.

We would like to express our gratitude to staff in the National Park, Marion McCahon and Arthur Hannan, for their local knowledge of Glenbranter and Sallochy. We thank Mr. David Anderson of the Forestry Commission for providing expert knowledge on the study areas in this project. His advice made this project possible.

Finally, I (WP) would like to thank members of my family (Angela, Dylan and John) for providing their company in the field while carrying out the collection of scats and squirrel surveying.

REFERENCES

- Arnold, H. R. (1993). *Atlas of Mammals in Britain*. Institute of Terrestrial Ecology, Natural Environment Resource Centre, London.
- Balharry, D. (1993). Factors affecting the distribution and population density of pine martens in Scotland. Unpublished PhD Thesis, University of Aberdeen.
- Bang, P. and Dahlstrøm, P. (2001). *Animal Tracks and Signs*. Oxford University Press, Oxford.
- Battersby, J. (2005). *UK Mammals: Species Status and Population Trends*. JNCC/Tracking Mammals Partnership.
- Bierman, S. J., Fairbairn, J. P., Petty, S. J., Elston, D. A., Tidhar, D. and Labin, X. (2006). Changes over Time in the Spatiotemporal Dynamics of Cyclic Populations of Field Voles (*Microtus agrestis* L.). *The American Naturalist* 167, 583-590.
- Bright, P. W. (2000). Lessons from lean beasts: conservation biology of the mustelids. *Mammal Review* 30, 217-226.
- Chinery, M. (1993). Collins Field Guide to Insects of Britain and Northern Europe (3rd Edition). Harper Collins Publishers, London.
- Day, M. G. (1966). Identification of hair and feather remains in the gut and faeces of stoats and weasels. *Journal of Zoology* 148, 201-217.
- de Jounge, J. (1981). Predation of the pine marten in relation to habitat selection and food abundance during winter in central Sweden. in: Corbet, G. B. and Harris, S. (1991). *The Handbook of British Mammals* (3rd Edition). Blackwell Science Ltd, Oxford.
- Erlinge, S., Goransson, G., Hansson, L., Hogstedt, G., Liberg, O., Nilsson, I. N., Nilsson, T., von Schantz, T. and Sylven, M. (1983). Predation as a regulating factor on small rodent populations in southern Sweden. *Oikos* 40, 36-52.
- Gurnell, J., Lurz, P. and Pepper, H. (2001). *Practical Techniques for Surveying and Monitoring Squirrels*. Forestry Commission, Edinburgh.
- Gurnell, J. D., Venning, T., MacCaskill, B. and MacCaskill, D. (1994). The food of pine martens (*Martes martes*) in West Scotland. *J. Zool. Lond.* 234, 683-685.
- Halliwell, E. C. (1997). *The Ecology of Red Squirrels in Scotland in Relation to Pine Marten Predation*. Unpublished PhD Thesis, University of Aberdeen.
- Harris, E. and Harris, J. (2002). Field Guide to the Trees and Shrubs of Britain. Readers Digest Assocation Ltd., London.
- Helldin, J. O. (1999). Diet, body condition, and reproduction of Eurasian pine martens *Martes martes* during cycles in microtine density. *Ecography* **22**, 324-326.
- Holm, J. (1994). *Squirrels*. Whittet Books Ltd, London.
- Kenward, R. E., Hodder, K. H., Rose, R. J. and Walls, C. A. (1998). Comparative demography of red squirrels (*Sciurus vulgaris*) and grey squirrels (*Sciurus carolinensis*) in deciduous and conifer woodland. J. Zool. Lond. 244, 7-21.

- Lockie, J. D. (1964). Distribution and Fluctuation of the Pine Marten, *Martes martes* (L.), in Scotland. *The Journal of Animal Ecology* 33, 349-356.
- MacDonald, D. (2001). *The New Encyclopedia of Mammals*. Oxford University Press, Oxford.
- Mitchell, J. (2005). Grey squirrels and pine martens at East Loch Lomondside. *The Glasgow Naturalist* 24: 62.
- Morris, P. A. (1993). A Red Data Book for British Mammals. The Mammal Society, London.
- Nyholm, E. S. (1970). On the ecology of the pine marten (*Martes martes*) in Eastern and Northern Finland. *Suomen Riista* 22, 105-118. in: Corbet, G. B. and Harris, S. (1991). *The Handbook of British Mammals* (3rd Edition). Blackwell Science Ltd, Oxford.
- Pepper, H. and Patterson, G. (1998). *Red Squirrel Conservation*. Forestry Commission, Edinburgh.
- Ross-Craig, S. (1956). *Drawings of British plants*. G. Bell & Sons Ltd, London.
- Russell, A. J. M. and Storch, I. (2004). Summer food of sympatric red fox and pine marten in the German Alps. *Eur. J. Wildl. Res.* 50, 53-58.
- Teerink, B. J. (2003). *Hair of West-European Mammals*. Cambridge University Press, Cambridge.
- Trubridge, M. (1993). Pine Martens at Inversnaid, Loch Lomondside. *Scottish Bird News* 29.
- Wauters, L. A., Gurnell, J., Preatoni, D. and Tosi, G. (2001). Effects of spatial variation in food availability on spacing behaviour and demography of Eurasian red squirrels. *Ecography* 24, 525-538.
- Webster, J. A. (2001). A review of the historical evidence of the habitat of the pine marten in Cumbria. *Mammal Rev.* 31, 17-31.